On the Mechanical Origin of the Dentition of the Amblypoda.

By E. D. Cope.

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As the Amblypoda form the only order of ungulate Mammalia with tritubercular superior and tuberculo-sectorial inferior molars, the question has arisen in my mind why they did not develop a sectorial dentition in the same way, and for the same mechanical reasons, that the unguiculate series has done so. Having recently assigned* certain mechanical reasons for the evolution of the sectorial teeth of the Carnivora, it is necessary to explain why the Amblypoda, which had apparently the same mechanical conditions at the start, did not eventually produce the same result.

In the first place I observe in the families Coryphodontidæ and Uintatheriidæ of the Amblypoda, that the shearing the inferior molar crests against the superior molar crests, is from before backwards. In the Creodonta and Carnivora it is from behind forwards. I supposed the latter movement to be due in these animals to the wedging of the inferior canine in front of the superior canine, a movement undoubtedly sufficient to account for such a shearing, other things being equal. But in the Coryphodontidæ the canines are greatly developed, yet the shearing of the molar crests is in the opposite direction. It is also evident that the development of the canines cannot have been the cause of the maintenance of any kind of a shear between alternating parts of molar teeth, otherwise the quadritubercular type of molar would not have come into existence in such families as have large canine teeth, such as the Suoïd Artiodactyla. I do not for these reasons abandon the opinion that the development of the canines has not had a great deal to do with the development of the sectorial dentition. I only deny that it has been the cause of its *origin*, that is, of the anterior shearing of the lower molars on the upper, at its beginning.

The divergence of mammalian dentition into the two types, the tritubercular and quadritubercular, has been, as it appears to me, due to the adoption of different food-habits. The tritubercular is the primitive, and is adapted for softer food, as flesh, so that primitive placental Mammalia were carnivorous or nearly so. The mastication of hard food was impossible until the molars of the two series opposed each other, and this was not accomplished until the quadritubercular superior molar was produced. This was accomplished, as I have pointed out, by the addition of a posterior internal tubercle, and I suspect that the mechanical cause of its origin was the attempt of the animal in mastication to crush substances harder than flesh against this posterior edge of the superior molar, by applying to it the anterior edge of the lower molar. In the devouring of flesh this movement is not necessary or only necessary so far as to produce a shear-

* The Mechanical Origin of the Sectorial Teeth of the Carnivora. Proceeds. Amer. Assoc. Adv. Sci. 1887, p. 254.

ing movement to cut a resisting ligament or tendon. The different mechanical movements in the two cases were due to the manipulation of its lower jaw by the animals, just as we may see them to-day endeavoring to masticate substances in accordance with their hardness, form, etc. It would appear in the case of the tritubercular superior molar, that the impact during the effort to masticate hard and tough substances, as vegetable tissues, and seeds, has had its usual effect to stimulate deposit of material. The shearing movement has had an opposite effect, viz., that of wearing away the surface subjected to it, and the flattening of the sheared face. That the development of the grinding mastication should take place in ungulate Mammalia is entirely appropriate to the structure of their digits; the hoofed structure unfitting them for the seizure of living prey.

In the Amblypoda, however, we have a hoofed order in which the primitive tritubercular superior and tuberculo-sectorial inferior molar remained. Of the three families, the latest, the Uintatheriidæ, display the greatest anomaly, while the earliest, the Pantolambdidæ (of the Puerco) give the simplest known type. It is to the intermediate family, the Coryphodontidæ of intermediate age (the Wasatch Eocene) that we must first look for the explanation of the peculiar characters of the order.

Before doing so I give an explanation of the various mechanical types of mastication:

I. Part or all of inferior molars work between superior molars. Amœbodect mastication.

1. The inferior molar shears forwards on the superior molar. Proterotome mastication; Creodonta, Carnivora.
2. The inferior molars shear posteriorly against the superior molars. Opisthotome mastication; Coryphodontidæ, Uintatheriidæ.

II. Molar teeth of both jaws oppose each other. Antiodect mastication.

3. The movement of the lower jaw is vertical. Orthal mastication; Suoïdea, Tapiridæ.
4. The movement of the lower jaw is from without inwards. Ectal mastication; many Perissodactyla.
5. The movement of the lower jaw is from within outwards. Ental mastication; most Artiodactyla; some Perissodactyla.
6. The movement of the lower jaw is from before backwards. Proal; most Rodentia.
7. The movement of the lower jaw is from behind forwards. Palinal; Proboscidia (Ryder).

The methods of mastication of Division I may be also defined by the terms of Div. II. Thus the proterotomes are all orthal, and I will show that the opisthotomes are also ectal. Some of the orthals are opisthotome, as the Tapiridæ.

The peculiarities of the Pantodont and Dinoceratous dentition may be now taken up in order, and their mechanical causes assigned so far as possible. *In limine* I take the position that the mastication of the Amblypoda was accomplished by the transverse movement of the lower jaw across the upper, and that this is, therefore, the only order in which such mastication was performed by the primitive dentition, *i. e.*, the tritubercular and tuberculo-sectorial. That this is the type of mastication is suggested, but not proven, by the anisognathism of the dental system. But it is proven by the mark or path made by the posterior external cusp of the inferior true molar across the crown of the superior molar in the Coryphodontidæ. This cusp struck the posterior side of the rudimental anterior external lobe, and passed transversely across the crown (diagonally to the principal cross-crests), and slid up the apex of the internal cusp, producing the externally directed angle in its wear, seen in all specimens of the genera Metalophodon, Coryphodon and Ectacodon (Fig. 3). I also suspect that this movement is ectal, since the directions of the V's of the two dental series will permit no other. An at-

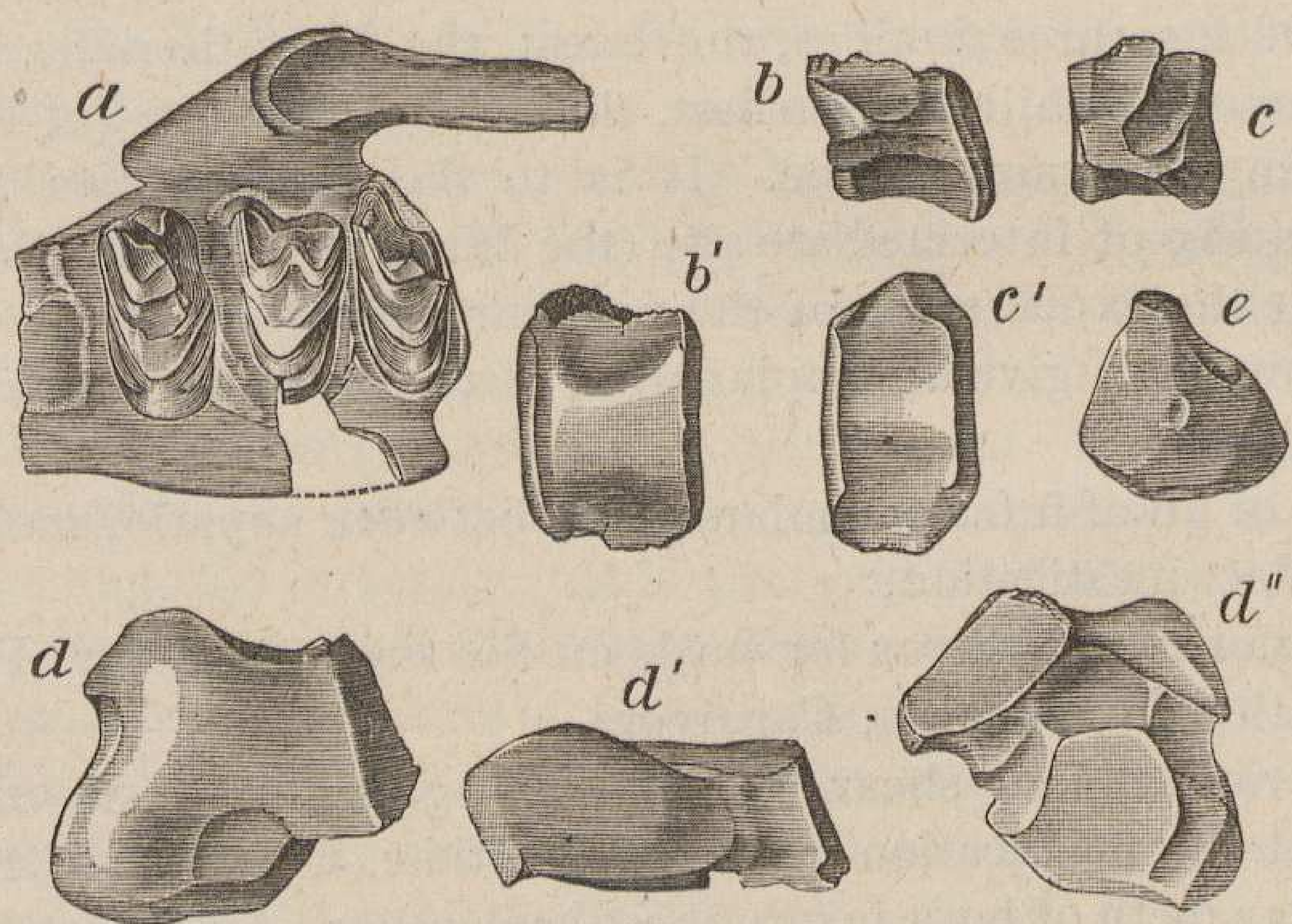

Fig. 1.—Bones and teeth of *Pantolambda bathmodon* Cope, two-thirds nat. size. From the Puerco beds of New Mexico. Fig. *a*, part of maxillary and malar bones from below, showing true molars, all somewhat broken. Figs. *b* and *c*, cervical vertebræ, left side; *b′* and *c′*, do. from below. Fig. *d*, astragalus from above; *d′*, from front, showing facet for cuboid; *d″*, from below; *e*, navicular bone from below. Original, from Report U. S. Geol. Surv. Terrs., F. V. Hayden.

tempt at an ental movement results in a jamming of the V's into each other, and further progress is impossible. It may be objected that the presence of the large superior canines forbids any considerable lateral movement of the lower jaw. The superior canines are however so divergent in the Coryphodontidæ that such movement is possible, and the transversely convex wear of these teeth proves just such a movement of the inferior canines on them. The lateral movement in the old males of the Dinocerata has been much restricted, but in younger males and females it was possible.

A second proposition is demonstrated by the discovery of the Pantolambdidæ. This is, that the superior molars of both the Coryphodontidæ and Uintatheriidæ are derived from a type with two external V's (Pantolambda, Fig. 1), and I propose to show how this derivation has been accomplished, and under what mechanical necessity. Pantolambda also

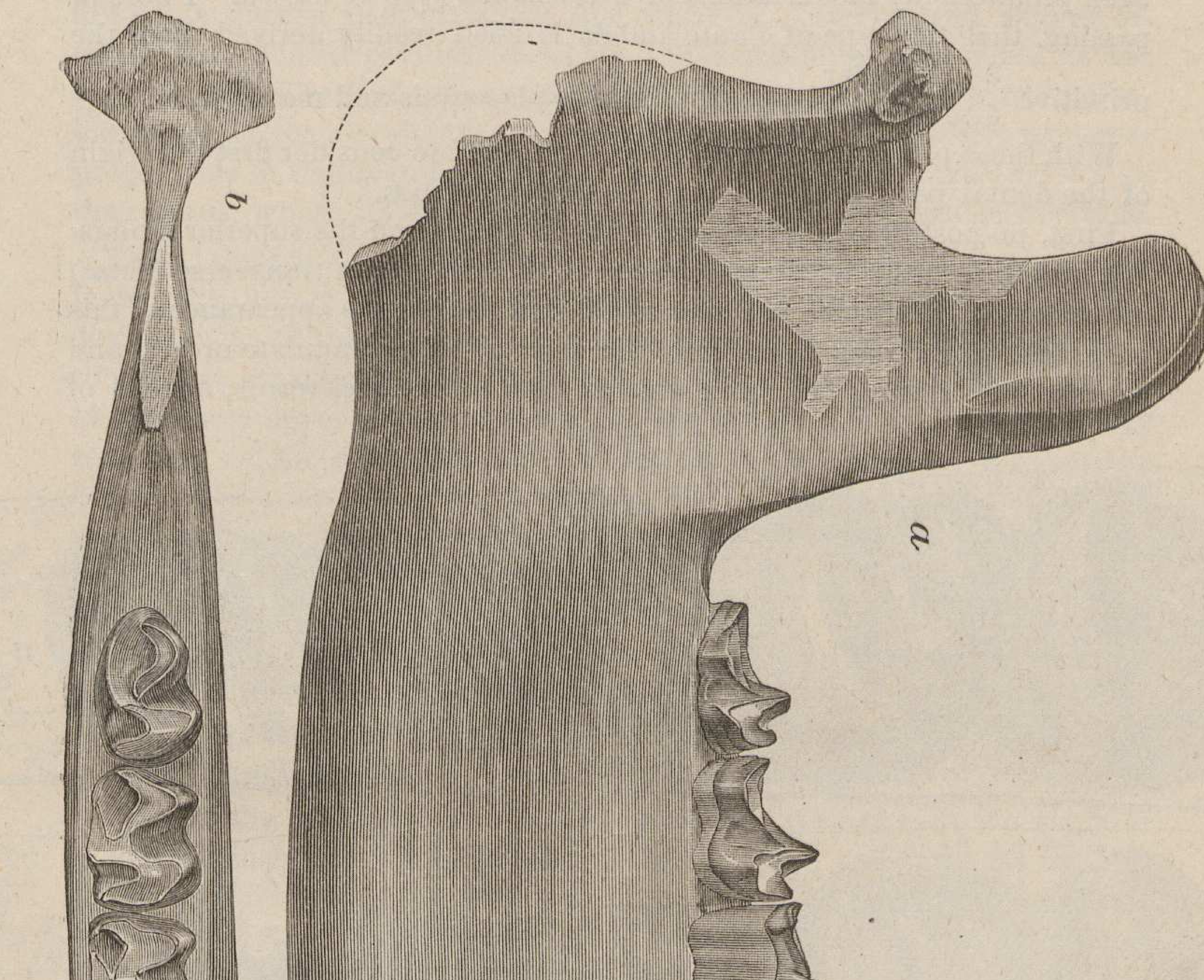

FIG. 2.—*Pantolambda cavirictus* Cope, mandibular rami, two-thirds natural size. Fig. *a*, right ramus for outer side. Fig. *b*, left ramus from above. From the Puerco bed. Original, from Vol. iii, Report U. S. Geol. Survey Terrs., F. V. Hayden in charge.

shows that the inferior molar structure of the two types mentioned has been produced by modifications of a W-shaped type of crown. I note in passing, that the type of Pantolambda is itself readily derived from the primitive $\frac{\text{3-tubercular}}{\text{5-tubercular}}$ type of primitive placentals and marsupials.

With these propositions established, I proceed to consider first the origin of the dental peculiarities of the CORYPHODONTIDÆ.

First, no posterior inner tubercle was developed on the superior molars. We may regard this as a consequence of the fact that a transverse (ectal) movement of the lower jaw was established before the appearance of this cusp, instead of after it, as was the case in other ungulate orders, and because the shearing has been always from before backwards, instead of

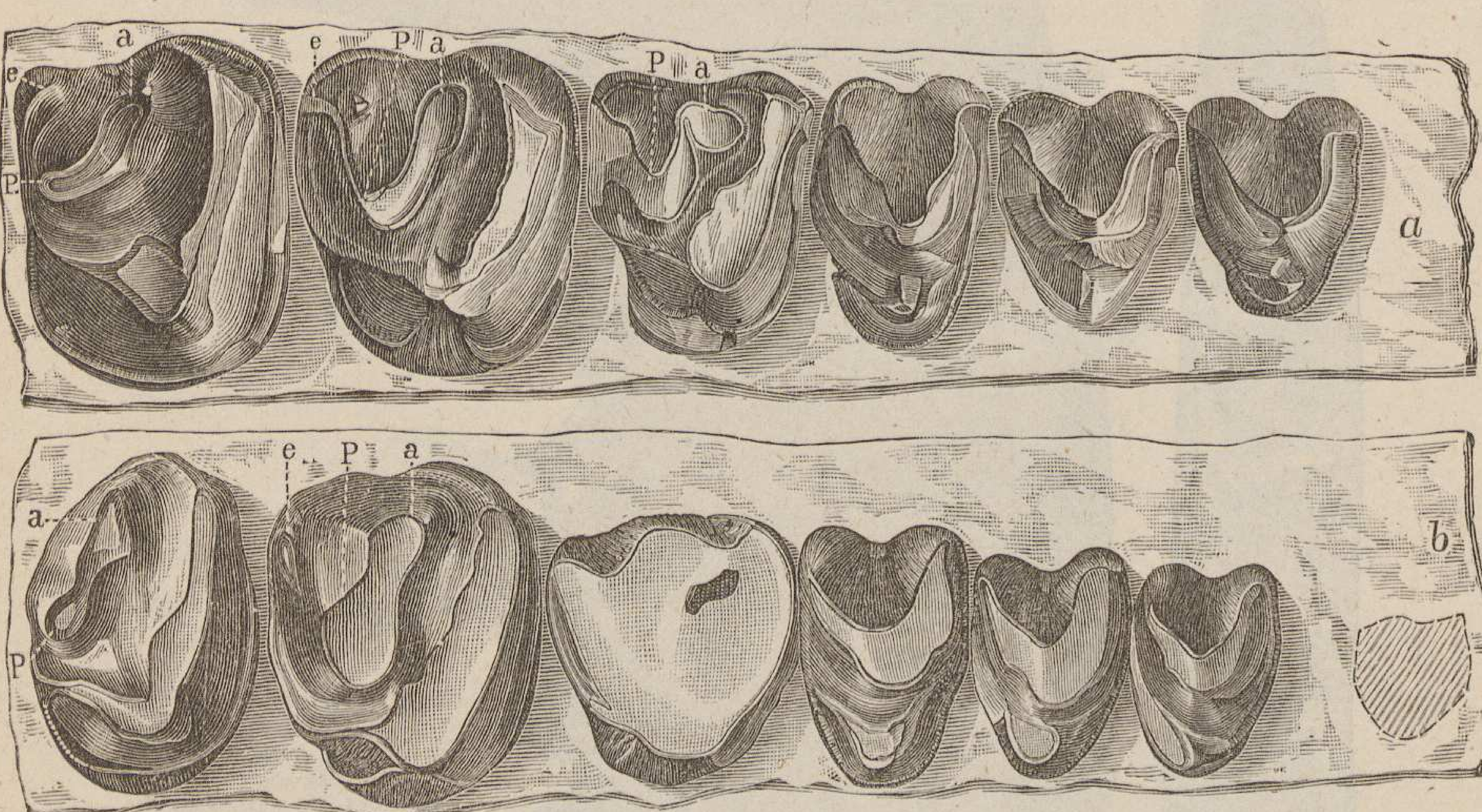

FIG. 3.—Superior molar series of Coryphodontidæ, two-thirds nat. size, from the Wasatch beds of Wyoming. Original. Fig. *a*, *Ectacodon cinctus* Cope. Fig. *b*, *Metalophodon testis* Cope.

overlapping from behind forwards, as in all other Ungulata. The stimulus already assigned as the cause of the development of the fourth tubercle is, under these circumstances, wanting. (Fig. 3.)

Second, the anterior cingulum, which extends from the internal cusp to the anterior external angle of the crown along its anterior base, is greatly developed. This may be reasonably ascribed to the stimulus produced by the friction of the posterior limb of the anterior V of the inferior molar in the transverse movement in mastication. The anterior crest of the superior molar is developed instead of the corresponding posterior crest of the superior molar in front of it, because the transverse movement of the inferior molar follows a path much more nearly coinciding with the anterior crest of the superior molar than with the posterior crest. That is, it follows a curved path of which the centre is posterior, and near or between the glenoid cavities on which the mandibular rami move, as has been described by Ryder in various other ungulates.* This is the probable cause of the development of this crest from its originally moderate proportions in Pantolambda (Fig. 1), and from the unknown ancestor of that genus, where its dimensions are presumably still less considerable.

Third, the anterior external tubercle or V is reduced to a conical rudiment (Fig. 3 *a*). This is evidently due to the disuse following the great development of the anterior cingulum which extends from the internal tubercle to the anterior external angle of the crown. A similar but less considerable development of this ridge is accompanied by a corresponding reduction of the anterior external lobe, in some genera of the Lophiodontid Perissodactyla. The reason why this V has been extinguished and not merely pressed backwards, is the fact that the posterior external V of the superior molar has retained its place, and has not given way to allow room for the anterior one. This V has retained its place partly on account of its remoteness from the source of pressure in front, but principally because it fits the posterior transverse crest of the lower molar in front, and the anterior oblique crest of the next succeeding lower molar behind, so that its use has been only possible in its primitive position.

Fourth, the posterior limb of the posterior external V of the superior molar is wanting on the last molar in Coryphodon, and from the last two in Metalophodon (Fig. 3). The absence of this crest from the last superior molar is due to the absence of a corresponding crest of the inferior molar (Fig. 4). This is the oblique crest at the anterior extremity of the inferior molar, and it shears against the posterior limb of the posterior external V of the superior molar, representing the sectorial blade of Carnivora. It is little elevated in the Coryphodontidæ, owing to the fact that it is little used, since the crests of the inferior molars shear backwards and not forwards on those of the upper. The effect of this disuse tends, in the history of the Coryphodontidæ, to become more and more evident. The non-existence of a fourth molar behind the third in the lower jaw, accounts for the absence of the crest in question from the last superior molar, while the absence of the same crest from the second superior molar of Metalophodon, indicates the absence or rudimentary condition of the corresponding crest of the corresponding inferior molar.†

* Proceedings Philadelphia Academy, 1878, p. 56.

† I have just detected an error in Plate xlvi, Tertiary Vertebrata, which has been copied in *American Naturalist*, 1884, p. 1198, by which the artist has drawn the left ramus mandibuli of *Bathmodon radians* in the place of the right one. The two rami are in the specimen separate from the symphysis, and the artist has simply drawn the ramus in connection with the wrong branch of the symphysis. I had not noticed this egregious blunder until the present writing, and no one else appears to have observed it.

The above four propositions cover the principal peculiarities of the dentition of the Coryphodontidæ. I now proceed to a consideration of those of the UINTATHERIIDÆ.

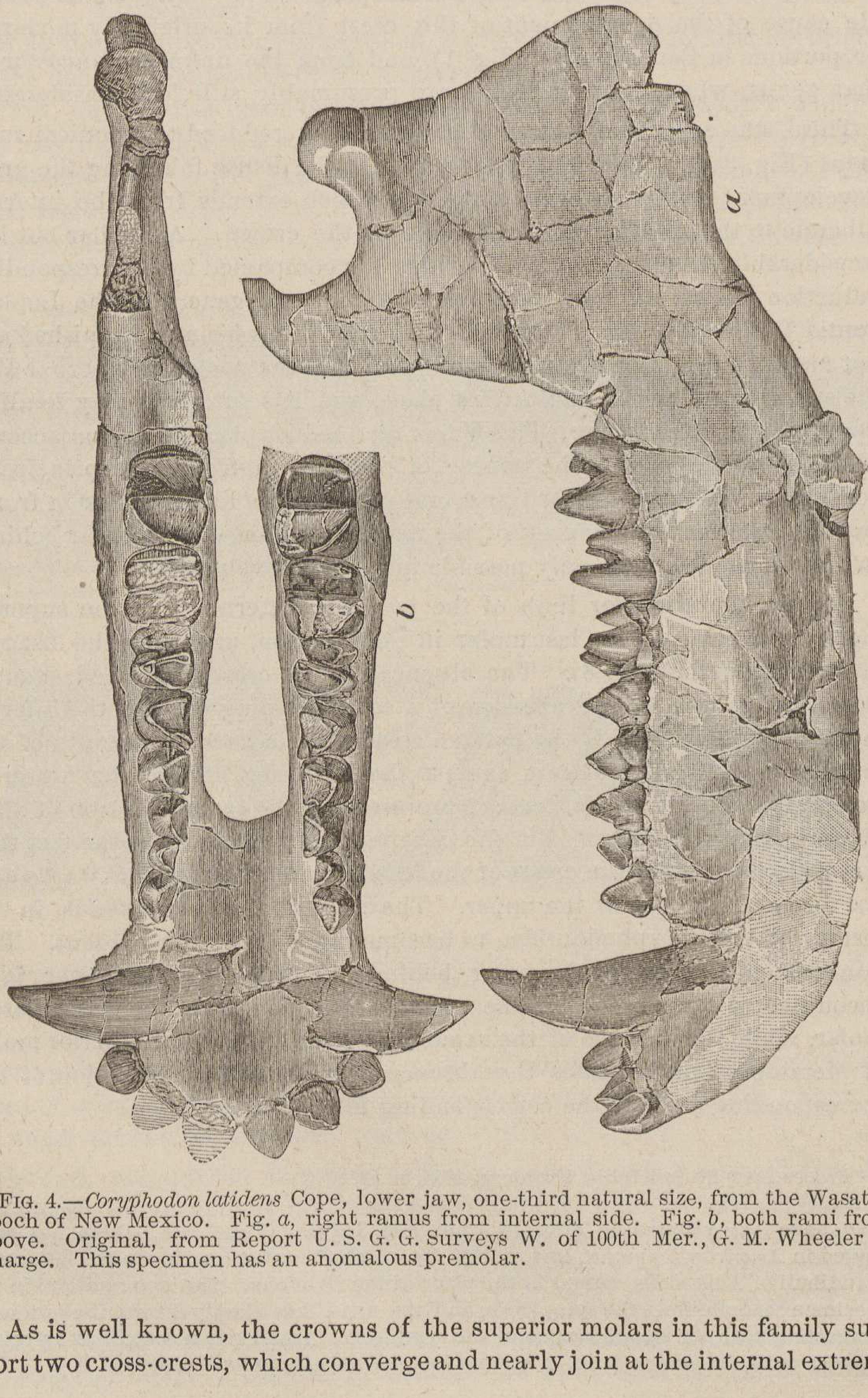

FIG. 4.—*Coryphodon latidens* Cope, lower jaw, one-third natural size, from the Wasatch epoch of New Mexico. Fig. *a*, right ramus from internal side. Fig. *b*, both rami from above. Original, from Report U. S. G. G. Surveys W. of 100th Mer., G. M. Wheeler in charge. This specimen has an anomalous premolar.

As is well known, the crowns of the superior molars in this family support two cross-crests, which converge and nearly join at the internal extremity of the crown (Fig. 5). The anterior of these crests is pretty clearly the anterior cingular crest of Coryphodon, but the homology of the posterior crest is less obvious. In order to determine this point recourse must be had to the inferior molars, which are more readily understood.

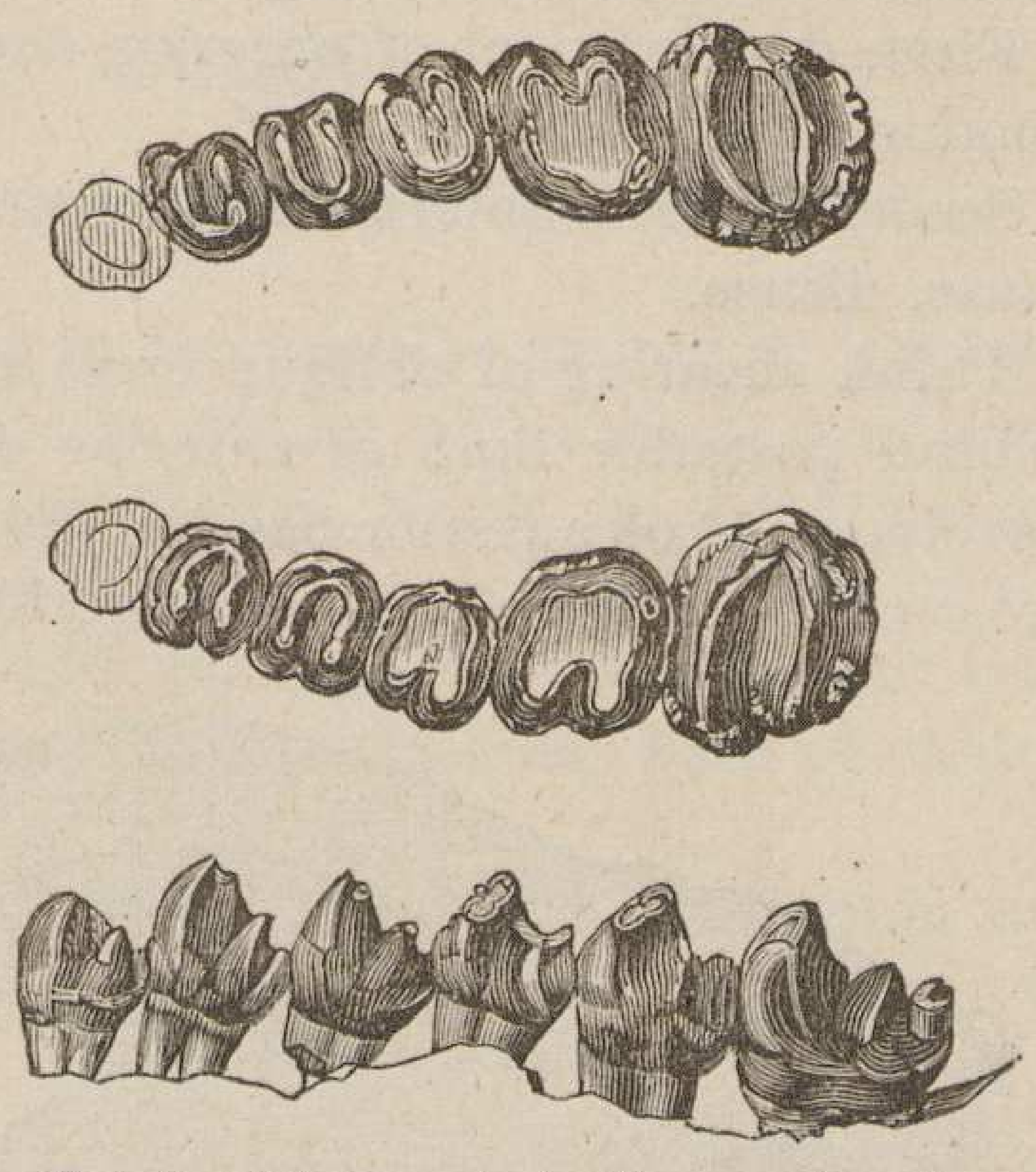

FIG. 5.—Dinocerata teeth, one-fourth nat. size. Upper figures superior molars of *Uintatherium leidianum*, one-fourth nat. size. Lower figure, inferior molars of jaw of another species of Uintatherium. From Osborn, memoir on Uintatherium and Loxolophodon.

In the lower molar of the Uintatheriidæ, we find the anterior triangle of the tuberculo-sectorial type, but with the anterior limb rudimental. The posterior part of the crown differs from that of the Coryphodontidæ in having no posterior transverse crest, but in its stead the diagonal crest which connects the external extremity of the posterior transverse with the interior extremity of the anterior transverse crest. This oblique crest wears the posterior crest of the superior molars on its anterior face, as the anterior transverse crest wears the anterior crest (cingular) of the superior molar on its anterior face. (Fig. 6).

Comparison with the dental structure of Pantolambda (Fig. 1-2), shows which crests of the two series stand in this relation to each other. The diagonal crest of the inferior molar in this genus shears in front of the posterior limb of the anterior V of the superior molar. Guided by this fact we may regard the posterior cross-crest of the superior molar of the Uintatheriidæ, as the posterior limb of the anterior external V. We must then suppose that the anterior limb of this V has disappeared from this type of molar, and the anterior cingular crest has taken its place, thus forming a long V with the posterior limb. The tubercle between the crests at their open external valley, may be a remnant of this external crest. A low tubercle on the crown behind the inner extremity of the posterior crest, may be a rudimental fourth tubercle, or even the apex of the posterior external V.

The homology of the posterior crest of the superior molar here proposed is sustained by the fact that there is no posterior transverse crest on the lower molar.* Had the crest in question been part of the posterior V of the superior molar, the posterior crest of the inferior molar would have had use, and would not have disappeared.

If this homology is correct, the Dinocerata were derived directly from the Pantolambdidæ, and not through the Coryphodontidæ.

* The raised heel on these inferior molars is not the posterior transverse crest.

The mechanical causes of the peculiarities of the Dinoceratous dentitions are then the following :—

First, development of anterior cingular crest ; cause same as in Coryphodontidæ.

Second, loss of anterior limb of anterior external V of superior molars ; cause, disuse.

Third, shearing of oblique crest of inferior molar in front of instead of behind posterior limb of anterior external V of superior molar. Cause, development of anterior basal cingulum of superior molar, which wedges cross-crests of inferior molar anteriorly.

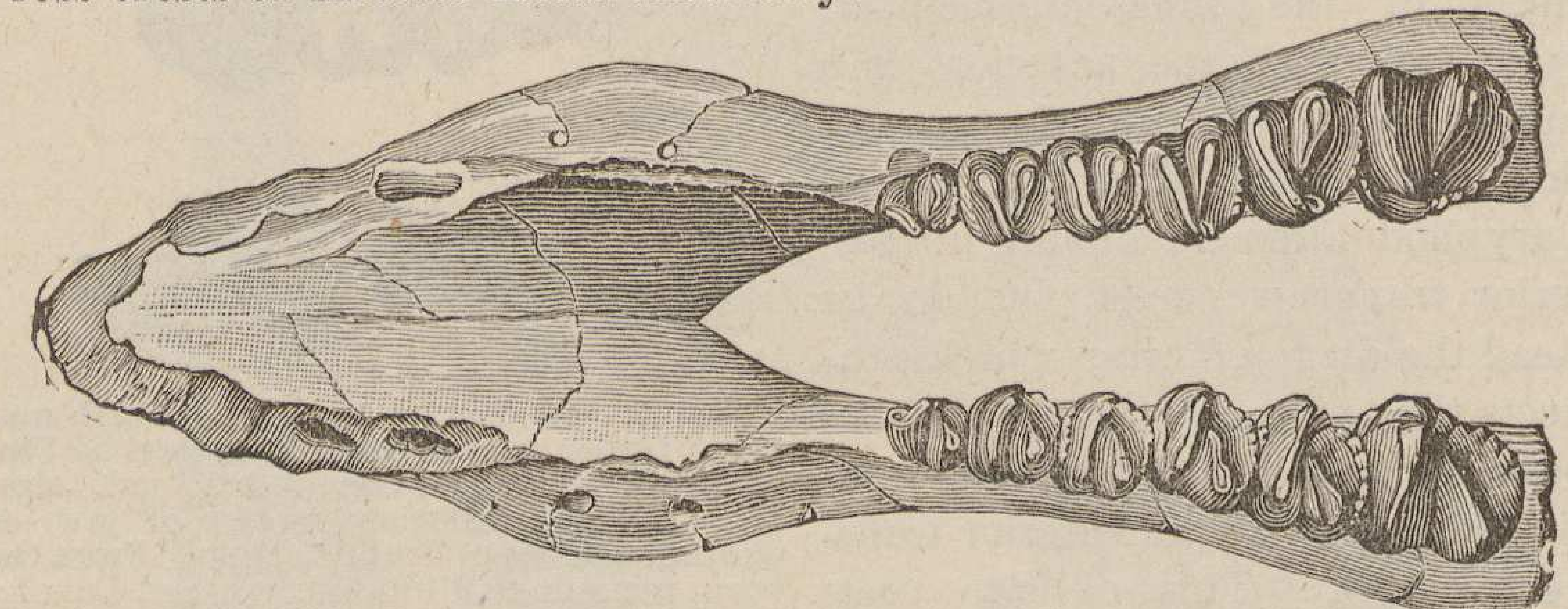

Fig. 6.—Uintatherium, mandible anterior to coronoid process, one-fourth nat. size; from Bridger beds of Wyoming. From Osborn, memoir on Loxolophodon and Uintatherium.

Fourth, loss of posterior cross-crests of inferior molars. The answer to this question is the answer to the other question, Why was the oblique crest of the inferior molar developed in the Uintatheriidæ while it remained rudimental in the Coryphodontidæ? The answer to these questions is the explanation of the principal peculiarities of the former family. The answer appears to me to be simply that while the movement of the lower jaw in mastication was probably ectal in the Coryphodontidæ, it was probably ental in Uintatheriidæ. This explanation is largely hypothetical, yet it accords with the relations between use and the development of the crests in the two families. In the ectal movement in Pantolambda the oblique crests of the opposing molars are soon separated from mutual contact, so that none of them have use on the internal half of the crown except the anterior cingular. In the ental movement, on the other hand, the limbs of the external V's are used to the utmost. The posterior limb of the anterior V is most used in Pantolambda, for the reason, as it appears to me, that the inferior molar is wedged forwards as it moves outwards in consequence of the guidance of the anterior cingular crest, and the wedge-shape of the triangular superior molar. While this causes the greatest use of the posterior limb of the anterior external V, it withdraws the posterior crest of the inferior molar from shear with the anterior crest of the posterior V, so that it has disappeared through disuse.

In general it may be observed, that the ental movement is the easier to the Dinocerata because the V's open exteriorly in both jaws. In the Pantodonta the ectal movement is easier, because the V's of the lower molars open interiorly.